ON THE HAUSTORIA OF THE ERYSIPHEAE

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The study of plant structure and development as a means of revealing relationships in plants appealed to botanists immediately upon the advent of the microscope, but the study of structure and development as a means of revealing functions is a more recent field of investigation which has already produced most valuable results. While the questions concerning the important functions of reproduction must be largely answered from the side of structure there are also other functions performed by vital organs too minute and too intangible for investigation by experiment. Careful observations of the changes occurring in the growing haustoria of a parasitic fungus must add to our special knowledge of the functions of the fungus, and to our knowledge of parasitism in general. That the progressive study of structure must to a large extent accompany inquiries in biology is well illustrated in the early literature on the Erysipheae, which was produced at a time when the possibilities of microscopic study were just beginning to be appreciated.

The investigation of the structure of the Erysipheae and the events leading up to the discovery of their haustoria

had to do in the beginning with economic considerations. In 1845, at Margate, England, Tucker was led to a study of a grape mildew on account of its simultaneous appearance with a disease of the leaves and fruit of the grape. The spread of the fungus kept pace with the symptoms of disease of the vine. The fruit over which the fungus spread usually cracked and swelled, at the same time emitting an unpleasant odor. The mycelium was found on the interior of the leaf, through the stomata of which, branches projected to the exterior, and bore sometimes simple, sometimes septate spores. Tucker's investigation led him to conclude that the fungus was a parasite upon the vines, and in an article[1] published in the Gardeners' Journal (1874), he figured the conidia and mycelium. It is difficult to believe that the fungus was one of the Erysipheae, but after this time Oidium Tuckeri was thought to have some intimate connection with the disease. From England the disease spread to France and appeared at Versailles[2] in 1848. By 1851 it had spread all over Europe. Losses to owners of vineyards became so great that in Italy commissions were appointed to investigate the disease. For several years there had been much active work in a systematic way on the powdery mildews, and Von Mohl[3] set for himself the task of determining

1. Reviewed in the Gardeners' Chronicle: 48. 1847. Also in Bot. Zeit. 1848. p. 376.

2. Bouchardat in Compt. rend. XXXIII, 145.

3. Die Traubenkrankheiten. Bot.Zeit.1852,pp.9-and 31.

whether the fungus caused or followed the grape disease, since the disease had been ascribed by Robineau[1] to an insect. Von Mohl did not record his methods of investigation except to state that he examined the interior of the fruit under a microscope (l.c.p.14). In this connection he noted the cracking of the larger grapes when covered by fungus. His search in the interior tissue of the fruit did not reveal the presence of the fungus there, so he concluded that the fungus produced its effects through the epidermal cells. Upon the epidermal cells of the young leaves, flowers and fruit there were to be seen, as soon as the fungus became visible, brown spots which spread as the fungus spread. Young fruit upon which the fungus appeared did not reach maturity, but withered and died. His conclusion is (l.c.p.13): "Diese Umstände machen es wahrscheinlich dass der Pilz die Pflanze, auf der er wächst, erst krank macht, die Säfte der oberflachen Zellen zersetzt und ihr Wachsthum benachtheiligt, auf analoge Weise wie Achlya prolifera im Wasser lebende Thiere, auf denen sie sich festsetzt, krank macht, wie Merulius destructor im abgestorbenen Holze Zersetzung hervorruft."[2] In 1853 Von Mohl made a serious study of the weather conditions under which the fungus was able to accomplish such destruction. He

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1. Compt. rend. XXXIII, p. 313. Bot. Zeit. 1851, p. 839.

2. Bot. Zeit. 1853, p. 585. Tf. XI.

examined the infested leaves more carefully and learned that the brown spots on the leaves appeared wherever the fungus was attached to them. He found that at the brown spots the mycelium threads produced irregular out-growths for attachment, which he called "Haftorgane." Von Mohl strongly objected (p. 587) to the report of Amici, of the Italian commission, who believed the appearance of mildew on the grape to be a proof of disease in the plant rather than the cause of the disease. The former cited as support to his proposition,that the mildew produced the disease, the opinions of Prof. Visiani and Dr. Zanardini of the Venetian commission as set forth in the Gazzetta ufficiale di Venezia (June 1, 1853). Zanardini (1851) had observed the protrusions by which the fungus appeared to attach itself and called them fulcra. Von Mohl credits Zanardini with the discovery of these "Hatforgane." According to Von Mohl (p. 594): "Visiani glaubt nähmlich gefunden zie haben, dass diese Haftorgane nach Art von Wurzeln in das Gewebe der Epidermis eindringen." But Von Mohl did not believe Visiani's opinion to be the correct one. He could see only the surface organs of attachment. Concerning the cells beneath the "Haftorgane" he observed: "Der Inhalt.... färbt sich bräunlich ballt sich unregelmässig(zusammenund) es nimmt auch die Wandung der Zelle eine braune Färbung an, welche besonders an den Seitenwandigen stark hervortritt."

It seems probable then that Visiani was the first to recognize what we now call haustoria, and in his comparison of them to the roots of higher plants he was the first to obtain a conception of those functions through which the parasite nourishes itself. Thus,as the structure of the fungus became better known, the general notion of parasitism took more definite shape.

De Bary[1] seems to have been the first to work out the structure of haustoria.[2] He applied the name, however, both to the exterior organs of attachment and to the absorbing organs of the fungus which he found within the epidermal cells of the leaves (Anthriscus silvestris, Angelica silvestris and Trifolium medium). Frank, at a later date (l.c.p.), very well named the "Haftorgane" appressoria,reserving the term haustoria for the organs of absorption. Of appressoria De Bary distinguished three sorts (p.26): (a) haustoria exappendiculata,"bei allen untersuchten Formen von Sphaerotheca, Podosphaera, und den Ery-

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1. Beitr. zur Morphologie und Physiologie der Pilze. Dritle Reihe, Erysiphe: 23-52, Tf. IX-XI.1870.

2. The admirable work of the Tulasne brothers in the Ann. sc. nat. (Ser.III. Tome XV) and of Leveille (Ib.) has not been accessible to me. It seems impossible that there should have been no investigation of these organs between the time of Visiani and that of De Bary.

siphe- formen mit zweisporigen Asci," (b) h. appendiculata, and (c) h. lobulata. In his Comparative Morphology and Biology of the Fungi,[1] De Bary gives a general account of the mycelium and haustoria, based on his previous observations. He applies the name haustoria to all those "special organs of attachment and suction to be found in the Peronosporeae, Piptocephalis, the Uredineae and the Erysipheae." In regard to the last he says: "The mycelial filaments of the Erysipheae are furnished with transverse walls, and their numerous but distant branches spread themselves over the epidermis of phanerogamous plants, being generally closely applied to it, but at the same time easily separable from it. At certain circumscribed spots, however, they are firmly attached to the substratum, and in these spots they are provided with a haustorium, which, springing as a branch from a cell of the mycelium in the form of a very delicate tube, pierces the outer wall of the nearest cell of the epidermis and enters its cavity; there it enlarges into an ellipsoidal or somewhat elongated vesicle filled with protoplasm, which in Erysiphe graminis is branched in a peculiar manner."

De Bary's contributions to the knowledge of the Erysipheae have remained the most important until recent years. He describes the haustoria of Erysiphe Communis[2] thus:

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1. Translated by Henry E.F.Garnsey. Revised by Isaac Balfour. 1887. pp. 18-20.
2. Beiträge p. 26. Tf. IV, fig. 18. Podosphaera Castagnei on Melampyrum silvatium.

"In dem einfactsten Falle vollständiger Ausbildung stellen diese äusserst dünne röhrenförmige Ausstülpungen dar, welche auf der Berührungsfläche mit der Epidermis entspringen, unter ihrer Ursprungsstelle die Aussenwand der Epidermiszelle durchbohren in den Innenraum letzterer eindringen und hier, nach kürzerem oder längerem Verlaufe zu einer ei- oder keulen-förmigen, manchmal etwas gekrümmten Blase an-schwellen. Bis zu dem Punkte, wo sie sich in letztre erweitern, sind die Röhrchen von einer ebenfalls röhrenförmigen derben Fortsetzung der Epidermis - Aussenwand, wie von einer Scheide umgeben, daher scheinbar dickwandig; von der Epidermis - fläche aus, also in ihrem Querprofil gesehen, einen kleinnen hellen Kreis, der von einem breiten glänzenden Ring ungehen wird darstellend. An der Erweiterungsstelle geht die Scheide, rasch dünner werdend, in den Aussencontour der Blase über. Diese ist, wenn erwachsen, meist so breit oder breiter als der Querdurchmesser der myceliumfäden, von einer in der Jugend sehr zarten, in späteren Enwickelungsstadien aber deutlich doppelt contourirten farblosen Membran umgeben, und erfüllt von feinkörnigen Protoplasma, das entweder überall zeimlich gleichförmig aussieht oder in der Mitte einen dichten Ballen erkennen lässt, der von durchscheinenderem körnigem Plasma rings umgeben wird. Bei notorisch alten Exemplaren ist oft der ganze Inhalt der Blase zu einem homogenen fettglänzenden Klumpen

zuzammengeschrumpft." This description was a great advance from the results of previous investigators, and, considering his methods and the appliances available to him, is a very accurate one. It is to be noticed that his studies of the haustoria were all made from the surface of the leaves.

Büsgen[1] refers to haustoria in reporting upon his observations of chemotropic and other stimuli on the germinating tubes of fungi. He germinated conidia of Erysiphe communis from leaves of Polygonum aviculare on slides under cover-glasses. In some cases he used sections of infected leaves in weak nutrient solutions. He was able to obtain appressoria-like structures where the filaments came in contact with the cover glass, but the germinating tubes had a very limited growth and soon perished. His results with the leaves indicated chemotropic reactions in the filaments. As a whole, his experiments on the Erysipheae were unsuccessful and they bear little relation to the haustoria themselves. Reference will be made to this paper again in discussing Phyllactinia.

Galloway devotes a short paragraph to haustoria in an account of his "Observations on the Development of Uncinula spiralis,[2] and figures them in much the same way as

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1. Ueber einige Eigenschaften der Keimlinge parasitischen Pilze. Bot. Zeit. 5: 53. Tf. 1893.

2. Bot. Gazette 20:487. pl.XXXII. 1895.(Uncinula necator.)

De Bary. Finally, Harper very briefly describes haustoria in a paper, "Ueber das Verhalten der Kerne bei der Fruchtentwickelung einiger Ascomyceten."[1] His remarks on haustoria were confined to those of Sphaerotheca Castagnei, and he gives but a single figure. Palla[2] has recently investigated Phyllactinia on Berberis and Corylus, but he concerns himself with the habit and structure of the mycelium rather than of the haustoria. For the more minute points of structure his methods were inadequate, as he himself intimates.(p.70).

It will be seen from this brief resume of the literature that the minute structure and especially the development of the haustoria are almost entirely unknown.

Four fixing solutions were experimented with, and their respective merits were compared. Flemming's fluid (stronger solution), Merkel's solution, chromacetic acid (.7% of the former and .3% of the latter), and a saturated solution of mercuric chloride in .1% acetic acid were all chosen as likely to offer comparative advantages. Flemming's fluid proved the most reliable and satisfactory. In those cases in which it blackened the tissues, the sections, after having been attached to the slides, were bleached for twenty-four hours in hydrogen-peroxide. This method

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1. Jahrb. für wiss. Botanik. 29: 664. 1896.

2. Ueber die Gattung Phyllactinia. Ber.d. deutsch. bot. Ges. B. XVII. Heft. 2, 1899. p. 64-72. Tf. V.

furnished material which was uniformly well-preserved and capable of receiving a uniform stain. Merkel's solution was frequently satisfactory, but proved hardly as reliable for me as Flemming's. The other two solutions were far less satisfactory.

The material was washed from four to six hours in running water (that fixed in corrosive sublimate, from eighteen to twenty-four) and transferred to 95% alcohol through six stages, beginning with 15%, at intervals of 45 minutes at first, to two hours or more at the end. From absolute alcohol, the material was transferred in the usual way through a mixture of equal parts of absolute alcohol and xylol through pure xylol, through a saturated solution of 45% xylol, to pure 45% paraffin, and finally to 52% paraffin, in which it was imbedded. The sections of the leaves were cut 2/3μ in thickness and were fixed in series to the slides by a combination of the well-known albumen and distilled water methods. Some difficulty was experienced in sectioning those leaves which contain numerous large crystals of calcium oxalate, as Corylus and Xanthoxylum, as these crystals frequently caused the destruction of the ribbons. For that reason, the side of the leaf bearing the fungus was usually turned toward the knife, unless the fungus was amphigenous.

All staining was done on the slide. Wisselingh[1] finds in fresh material that chitin is present in many places as one constituent of fungus cellulose, and for the Erysipheae, chitin appears in the perithecia, appendages, mycelium, conidia, and conidiophores. He does not mention haustoria in this connection and finds no satisfactorily characteristic stain applicable to microtome sections of walls containing both cellulose and chitin. He finds, however, that congo-red in neutral and ammoniacal solutions stains pure cellulose dark; if chitin is present, the color is not dark unless he transformed the chitin to mycosin by heating the material (hermetically sealed in a glass tube containing K O H and immersed in oil) to a temperature of 160 C., for 20 minutes. He slowly removed the alkali by 95% alcohol[2] and the latter by water. Mangin[3] finds pectin

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1. Mikrochemische Untersuchen über die Zellwände der Fungi. Jahrb. für Wiss. Bot. 31, 1898. pp. 619-687. Tf. XVII u. XVIII.

2. This is a modification of Gilson's method. Das Chitin und die Membranen der Pilz zellen. Ber. d. Deutsch. chem. Gesellch., Jahrg. XXVIII. Heft 7.

3. Sur l'emploi du rouge de ruthenium en Anatomie vegetale. Compt. rend. T CXVI: 653. Mr 1893. Sur la structure des Peronosporees. Ib. T; 923. 1890. Sur la presence des composes pectiques dan les vegetaux. Ib. T. CIX: 579. 1889. Observations sur composition de la membrane chezles Champignons: Ib. T. CXVII: 816, 1893.

quite generally present in fungus cellulose, and employed ruthenium-red as a characteristic stain. Wisselingh (l.c. p. 632) was able to remove the pectin from cell walls containing it by heating them in a tube of glycerine, prepared as before, to a temperature of 300 C. Mangin did not investigate with reference to this question and Wisselingh denies the presence of pectin in this group. My own results confirm this view. With ruthenium-red as a stain the fungus did not stain at all, though the middle lamellae of the cells of the host-leaf gave the pectin reaction. The most characteristic staining obtained by me, in the use of congo-red-neutral and alkaline solutions - and methylene-blue - neutral and acid solutions - was an intense staining of the ascus wall in the perithecia. Wisselingh does not mention this as a part containing chitin, and, since the remainder of the mycelium stained much less darkly, it is possible that the ascus wall is composed of pure cellulose.[1] In this connection the discovery by Vosseler, that the inner layer of insects wings agrees in every respect with cellulose, is of special interest. Our knowledge of the constituents of cell walls leaves much to be desired and the successful application of Wisselingh's, or similar methods, to fixed material would be a valuable con-

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1. Ueber die Körperbedeckung der Insecten. Zoöl. Centrb. II: p. 117. 1895. Ref. Ver. vaterl. naturk. Württenberg. 50 Jhg. Sitzungsber. p. 85-86.

tribution to botanical technique. I find Flemming's well-known triple stain[1] of safranin, gentian-violet and orange-G very satisfactory. By this stain the nucleoli of the fungus and host are stained red, the chromatin, blue, and the ordinary protoplasm orange. Fungus nuclei in the process of division take the violet stain very readily, but those in a resting condition possess chromatin in very minute masses. The orange color is apt to predominate over the blue in such resting nuclei, because the amount of staining necessary to secure a violet color in the resting fungus nucleus generally results in over-staining the host tissues. Most of the figures of nuclei accompanying this paper were therefore made from preparations in which the violet stain was inconspicuous in them. I have represented the blue chromatin as very fine granules, however, because in properly stained sections it is visible as such.

Naturally, no fixed rule can be given for the length of time required for staining. The optimum method must be worked out for each host - a fact which adds to the difficulty of the investigation. If water is employed as a wash after safranin and gentian-violet, the sections need to

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1. Zimmermann A. Botanical Technique. Translated by J.E. Humphrey: p. 186. 1893. See also Neue Beiträge zur Kentniss der Zelle. II Teil. Archiv. f. mikr. Anatomie. Bd. 37: p. 685.

stain from 15 seconds to a minute or two; if acid alcohol is employed, from twelve to twenty-four hours are necessary. The concentrated orange was allowed to stain but a few seconds. The sections were then washed in absolute alcohol, cleared in clove-oil and mounted in Canada balsam.

Erysiphe communis proved very favorable for study, and since Erysiphe, Sphaerotheca, Microsphaera and Podosphaera appear to agree closely, as far as I have observed, in respect to their haustoria, I shall describe the fungus on Geranium as a basis for comparison. The quotation from De Bary sufficiently describes the origin of an haustorium. Fig. 8 represents such a case. A normal, mature haustorium contains, as a rule, one nucleus. The protoplasm proves to be of a spongy texture when stained and examined under the highest powers, and differs in no visible particulars from that found in the mycelial threads. The nucleus is similar to the nuclei everywhere found in the septate hyphae. Fig. 11 represents the only case I have observed of an haustorium with two nuclei.

By an inspection of Figs. 7 and 8 it may be seen that a thickening of the wall of the host cell surrounds and accompanies the neck of the absorbing organ for a distance. This collar is of different consistency from the wall from which it takes its origin, and usually stains but little, while the remaining portion takes the safranin

eagerly. The inner boundary of this little hollow cylinder adheres closely to the haustorium neck. Its outer boundary is represented by the middle circle in Figs. 17 and 20. This structure is constantly observable and accompanies the haustoria in nearly all cases. It is not always visible, however, as shown in Figs. 16 to 19. It is clear that, by the use of hand cut sections of fresh material and by a study of the haustoria from the leaf surface, De Bary was unable to make out the structure of this sheath fully. He says (p.28), "Nur fand ich nicht selten, dass auch in sonst normal aussehenden Epidermiszellen die blasige Auschwellung von einer dicken unregelmässig umschreibenen, der Wirthzelle angehörigen Protoplasmaschichte umgeben und selbst dergestalt verdeckt ist, dass sie erst nach Kali- der Ammoniak - einwirkung zum Vorschein kommt." This protoplasm-like sheath occurs very constantly, surrounding the haustoria. The outer contour is very delicate and has the appearance of a plasmic membrane. The material occurring between it and the real outer contour of the haustorium looks much like protoplasm. But it is not spongy like protoplasm, though it stains with orange. It is seen as a homogeneous, finely granular mass, or it most frequently occurs gathered into lumps of varying outlines which appear very minutely granular under the highest magnification. Figs. 19 and 8 illustrate this. In Fig. 8 the

middle cell contains an optical section of a haustorium. Within the center lies the relatively large nucleus with its large, red-staining nucleole and fine chromatin granules. Surrounding this is the spongy protoplasm staining orange. The whole is confined by the easily discernible haustorium wall, and between this and the delicate boundary of the sheath lies the material described by De Bary[1] as belonging to the protoplasm of the cell. Rosen observed in Puccinia asarina, growing in the intercellular spaces of Acarum, that the branched haustorium was connected with the host cell nucleus, in the majority of cases, and either adhered closely to it or entered it with disorganizing effects. Harper (l.c.p.664. Sphaerotheca castagnei) also thinks that this peculiar sheath indicated a similar condition - an agreement among the Erysipheae with what Rosen found in Puccinia, i.e., that there is an intimate connection between the nucleus of the host cell and the haustorium, and that this sheath was the disorganizing host cell nucleus. I have not found evidence of such a relation between haustorium and host nucleus in the Erysipheae. In the examination of many sections in search of stages in the development of the haustoria, it becomes more and more clear that the host nucleus and haustoria are indifferent to each

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1. Beiträge zur Kentniss der Pflanzenzellen. Beitr. zur Biol. Pflanzen. Heft. 2, VI: 237-266. Tf. II - III. 1893, p. 258.

other. The sheaths are present around the haustoria even if there are many in a cell, as frequently happens. In such cases if the cell is not so full of haustoria as to obscure the cell contents or crowd the host nucleus, it can be seen in a more or less normal condition. In the cells of hairs which are large enough to contain several haustoria easily, the sheaths of the haustoria can normally be seen while the host nuclei occupy some distant position in the cells. That the sheaths are not disorganized host cell nuclei can easily be demonstrated from microtome sections. The sheaths are to be accounted for in another way, as will be seen subsequently. It is to be seen in most of the figures that the host nuclei lie removed a greater or less distance from the haustoria. When, as in Fig. 16, the connection between the two is close, the nucleus is more or less disorganized. But the few cases I have figured make the proportion much too large to be in accordance with the facts. The sheath is not usually bounded by a tensely stretched membrane (Fig. 9 represents a special stage), but by a membrane having a more or less irregular outline, in section, beginning where the thick cellulose collar about the neck stops. The orange-staining contents are usually present in more or less abundance, except in E. graminis on Poa, where only the sheath is present and is sometimes inconspicuous. The triple stain is very useful

in this connection. The outer walls of the epidermal cells have an affinity for the safranin stain, but the collar about the haustorium neck stains much more delicately with it. In Fig. 10, represented because the cell was plasmolyzed, the collar is distinctly distinguishable from other parts and appears under the microscope very slightly stained by safranin. Again (in Figs. 8, 16 and 18, and frequently in other figures) the reaction of haustorium and cell wall upon each other was such that the neck of the penetrating organ is distinctly visible and its minute size appreciable; whereas, if it were not for this circumstance, the size of the tube would frequently be exaggerated. In an old and dinintegrating example the wall of the entire structure is often stained red.

The safranin stain frequently exposes the beginning of penetration. Nordhausen,[1] in experimenting with Botrytis cinerea, Penicillium and Mucor (p. 38) observed a marked browning of the epidermal cells in contact with the germinating spores. This always preceded penetration. He thinks (p. 7) that the phenomena of browning and subsequent death of the cell are due to some poison produced in the germinating of the spores. Von Mohl (l.c.p.592,1853), De Bary, Frank[2] and others mention this browning in the Erysipheae.

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1. Nordhausen. Beiträge zur Biologie parasitarer Pilze. Jahrb. f. wiss. Botanik. XXXIII: 1. 1898.

2. Die Krankheiten der Pflanzen. 1880, p. 556.

In the stained specimens this phenomenon is not conspicuous, though the cell wall about the point of penetration is more or less altered and dissolved. This is most conspicuous in E. graminis, and E. Cichoracearum on Eupatorium (Figs. 17 and 20). Seen from the outer surface, there is surrounding the point of penetration, an area which is entirely colorless, clear and shiny. The remaining portions of the epidermal wall stain with safranin. The outer contour of the wall seen in cross section is likely to be depressed in the area also, the depression being deepest at the point of penetration, as though a part of the cellulose had been dissolved away. This dissolution of the cellulose points to the conclusion that the Erysipheae produce an enzyme suited to this work. If this digested material is used for food by the fungus there would here be a correspondence with Nordhausen's observations on Botrytis. This food supply would then serve as a chemotropic stimulus in determining the production of the penetrating tubes, in addition to the nutrient material which may have exuded through the epidermis from the interior of the host cells at their cross walls. That these exudations do occur Büsgen has conclusively demonstrated (l.c. p. 59).[1] Evi-

1. Other investigators have made observations which support Büsgen's. Frank. Pflanzenkrankheiten: p.36. Behrens' Beiträge zur Kentniss der Obstfaule. Centrb. f. Bacteriologie, etc. Abth. II, Bd. V. p. 583.

dences of such exudations have not appeared in the course of this investigation, as the germination stages of the fungus would be the most favorable for the observation of such effects. The appressoria of the Erysipheae do not seem to prefer the cross walls. Nordhausen (l.c.p.11) adds to Büsgen's conclusions (that Botrytis penetrates at the cross walls, because there is a larger supply of material exuding there) the further observation that the structural conditions of the cross walls offer suitable places for mechanical and chemical attacks by the fungus. De Bary,[1] in 1886, isolated such a cellulose dissolving ferment. Ward (cit. p. 28) offers much circumstantial evidence that Botrytis possesses such a ferment. In the case of Erysiphe communis where the hyphae touch the epidermis or at certain points, if the hyphae and epidermis are in contact for a distance, there appears a deep reddening at the inner surface of the outer wall of the cell immediately under the point of penetration (Fig. 1). This is to be seen at times at the cross walls where haustoria are never developed. It is possible that this is the spot which gives the brown color in fresh material.

The next step to be observed in the development of the haustorium is the thickening of the wall of the epider-

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1. Ueber einige Sklerotien und Sklerotienkrankheiten. Bot. Zeit.: 377. 1886.

mis over an area coinciding roughly with the circle shown in Figs. 17 and 20. Nordhausen (p. 17) observed a slight effect of this kind with Botrytis cinerea on Tradescantia, Mnium, etc., but Ward[1] observed with the same species (apparently) which produced a lily-disease, an extraordinary swelling of the walls of the host, so that a large part of the lumen of the cells was filled. Nordhausen believes that the fungus used by him lives on the protoplasm of the poisoned cell chiefly. Ward is of the opinion that the fungus causing the lily-disease lives also on the gelatinized cell walls. In Erysiphe there does not appear to be a swelling of the wall so much as the addition of new material by the cell, because the collar formed from a part of this thickening remains permantly about the tube. At the same time with the thickening of the wall of the host cell, the growth of the penetrating tube is in progress. Its distal end enters the wall of the host cell, and, just at the point where the reddening of the wall previously appeared (Fig. 2) a very slight enlargement of the tube occurs, accompanied still by the reddening on either side (in longitudinal section, Fig. 2). But this does not bring the point of the tube into the lumen of the cell, for the thickening of the host cell wall keeps pace for a time

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1. On a Lily Disease. Annals of Bot. II: pp. 319-382. Pl. XX - XXIV, 1888. See Figs. 8, 57 and 58.

with the growth of the tube (Fig. 3). This penetrating tube is extremely minute. For Botrytis Nordhausen (p.39) found it to be 1/4 of the diameter of the ordinary hyphae. Miyoshi[1] has shown that the membrane penetrated effects the size of the tube. Thus, when collodion was used for a membrane, the tubes actually increased in diameter, while with an onion-skin there was no change in diameter. Ward's observations on this point agree with Nordhausen's. In all of the Erysipheae the penetrating tube is much smaller, as the figures show, and it is interesting to note that the nucleus of the absorbing organ must in some way make its way through this minute passage.

The tube (Fig. 3) continues its growth through the increasing or (as Ward thinks) swelling cellulose, a part of which remains permanently encircling the neck of the mature haustorium as the collar already mentioned. De Bary (Beitr. etc., p. 26) probably saw these structures. He says: "Nicht selten findet man, zumal bei dickwandiger Epidermis, auch an ganz alten, jedenfalls nicht mehr wachsenden Exemplaren Haustorien, deren Röhrchen die Epidermiswand eingedrungen ist, ohne im Innern zur Blase anzuschwellen, vielmehr sowohl seitlich, als am innern Ende umscheidet von einer Zapfen - oder buckelförmigen in das

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1. Die Durchborung von Membranen durch Pilzefaden. Jahrb. f. wiss. Botanak: 280, 1895.

Zellenlumen ragenden Vortreibung der Membrane (X,10)." Because of the closely connected series of stages which it is possible to secure, it is evident that these are not old, disintegrating haustoria. Rather they represent the beginnings of penetration. At any rate, if they represent dead haustoria they reveal the outlines of the cellulose parts none the less, and so tell the story of development.

Soon the tube, growing with increasing rapidity, overtakes the cell in what may be its efforts to protect itself against injury done by the fungus. Just what significance there is in this thickening of the host cell cannot be conclusively determined without experiment. Ward, as has been mentioned, found that Botrytis produced an extraordinary swelling of the walls of the lily. Since the collar of thickened cellulose remains permantly about the neck of the haustoria of the Erysipheae, it appears that the cell wall increases not only in bulk but in quantity also. That there does appear to be a swelling of a portion of the host cellulose at a later period will be seen presently. There are not data at hand to determine whether the penetrating tube by means of some chemical substance excites the cell protoplasm to unusual activity in the production of cellulose about the region of penetration or whether sharp points alone would cause such a production. Or,

again, it is conceivablethat the stimulating agent is the atmosphere acting through the wall at the point made thin by the work of the fungus. At any rate, the thickening of the host cell wall ceases after an ingrowth (U-shaped in outline) from the outer wall has been produced. The very delicately staining collar, making up the base of this ingrowth of cell wall, seems to end in the neighborhood of the place so easily observed in mature examples and gives place gradually or abruptly to a structure of a different consistency surrounding the still slender, growing tube (Fig.4). This U-shaped or papilla-like ingrowth of host cell wall seems to consist at this stage of two parts. The proximal portion (about one-third of the whole) is the part which afterward forms the collar of cellulose about the haustorium-neck. The distal end, on the other hand, takes faintly orange color from the stain; and it is slightly but minutely granular. It no longer has the appearance of ordinary cellulose such as appears in the host cell wall or in the basal collar. Some change has been wrought in it which has altered its consistency and its reaction to stains. No sharp boundary separates the proximal from the distal end. The two usually pass into each other gradually in the region indicated. A clear understanding of these facts is necessary for the proper comprehension of the nature of the sheathsof the haustoria, which will be

discussed subsequently. It is to be observed that the plasmic membrane of the host cell passes up the side and over the end of this cellulose in-growth.

It will be seen in Fig. 5 that the penetrating tube has taken a straight course through the cellulose thickening, a distance approximately equal to the length of the collar in a mature haustorium. From that point on to the time when its growth was checked by the fixing fluid the young haustorium has pursued a rather tortuous way or else the distal end of the ingrowth of cellulose has offered some resistance to the progress of the penetrating tube. The whole distal end of the cellulose ingrowth is distinctly granular and takes the orange stain. The end of the penetrating tube has begun to swell by this time. The nucleus has not yet started in. The staining of the host wall on the line of its inner surface is not seen, and, from this time on, the staining there is not usually visible. It is to be noticed that the hypha from which this tube arose is enlarged and flattened sufficiently to fall within De Bary's class of haustoria appendiculata peculiar to forms of this family with two-spored asci. Erysiphe communis, however, would be a species without appressoria according to such a classification. I question whether much dependence can be placed upon appressoria in systematic determinations, such as the separation of E. Galeopsidis[1] from E. Cichoracearum,

1. Ellis and Everhart. N.A.Pyrenomycetes: 14,1892.

the former is supposed to have lobed appressoria. The varieties of E. Galeopsidis used in this investigation do not appear to show a more conspicuous lobing of appressoria than represented by Fig. 5. Between the appressorium and the epidermal wall is drawn in outline a red-colored, cushion-like structure, not seen in other cases, and of which I am not able to explain the significance. In this case again the host cell nucleus is on the basal wall of the cell.

It is possible for the young haustoria to escape from this sheath which surrounds them above the collar - either by pressure, or fermentative action (or both). Fig.6 fairly represents such a case in a young example[1] and may be looked upon as an advanced stage over that in Fig. 5. Unfortunately, these stages are not numerous, and the one represented here is stained completely with safranin, probably because the main hypha had broken away and the haustorium is dying. Its contour is clear and entire, however, and degeneration has overcome only the protoplasmic contents as yet. It is within a thick-walled epidermal cell in the region of the mid-rib of the leaf. Outside is represented a piece of mycelium showing numerous globular safranin-staining bodies, which are probably food products of some sort.

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1. See Fig. for the same thing in an older example.

The bounding membrane of the haustorium sheath appears sometimes to show the osmotic qualities similar to those of the plasmic membrane of the host cell. Fig. 9 represents such a case. Here the granular contents so commonly seen have entirely disappeared except in some inconspicuous flocculent material. The disintegrated contents of the sheath have been entirely consumed. The bounding membrane outside is stretched and turgid. None of the solid portions of the contents of the host cell approach nearer to the body of the haustoria than the sheath membrane. That the membrane is tensely stretched shows that it must have been filled with a liquid substance when the piece of leaf was put into fixing fluid. Fig. 9 also shows that the passage of the nucleus through the penetrating tube into the body of the haustorium has in this case been delayed. We have, therefore, a vesicle nearly the size of the most mature haustorium filled only with spongy, vacuolated protoplasm. In the neck are two masses which stain with safranin. The exterior mass has at its distal end a portion staining very deeply, the remainder but slightly with orange. It is possible that the nucleus was on its way into the haustorium when its progress was checked by fixing. Or, it may be that the mass lying in front of it offers some obstruction to its progress. The passage of the nuclei into the haustoria is naturally most difficult to

observe. This doubtful case (Fig. 9) offers the only example observed. The hypha has been broken away so far that none of the pieces lying above the cell can surely be identified as belonging to this haustorium.

From what has already been said on the structure and development of the haustoria it is easy to understand the nature of the haustorium sheath and its bounding membrane. That is, the contents of the sheath consist of disintegrated cellulose from the distal end of the cellulose intrusionof the host cell wall through which the haustorium has made its way. The delicate bounding membrane of the sheath, on the other hand, is the plasmic membrane of the host cell, stretched and greatly enlarged by the osmotic forces involved in absorption by the fungus. There is abundant evidence from various sources in support of this view. Marshall Ward (l.c.p.356) has shown that Botrytis which caused the lily-disease investigated by him, produces a swelling and gelatinization of the cell walls of the lily leaves. Ward found that the fungus was able to live on this disintegrated cellulose. It is well known that certain bacteria produce ferments which are able to digest cellulose. Ward found such a ferment in Botrytis(pp. 343-346). So also Beyerinck[1] found that Coryneum Beyerinchii makes use of a dissolving ferment. Nordhausen (l.c.p.38) has shown

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1. Archives Neerlandaises, T. XIX, 1884, p. 43.

that Botrytis, Penicillium and Mucor can enter a cell wall and grow through it parallel to its surface for comparatively long distances. This power of disintegrating cellulose seems to be generally possessed by fungi, parasitic and saprophytic. The power possessed by pollen tubes of dissolving cellubose is well known.[1] There is also much evidence to be found in the study of the structure and development of the haustoria in support of the view that the contents of the haustorium sheath consists of disintegrated cellulose. That the Erysipheae possess the power of dissolving cellulose is easily understood. The partial dissolution of the epidermal wall of the host about the point of penetration has already been mentioned. The penetrating tube, it is seen, makes its way through a long ingrowth of cellulose before it expands into a mature haustorium. It has been mentioned that the mature stage shows no unmodified host cellulose surrounding the haustorium except the collar around the haustorium neck. The distal two-thirds of the papilla-like cellulose ingrowth partially disappears in the development of the penetrating tube. During its disappearance it undergoes changes which materially alter its microscopic appearance as concerns structure and its capacity of reacting to stains. The inner end of the in-

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1. Miyoshi. Ueberreitz bewegungen der Pollenschlauche. Bot. Zeit. Heft I, 1894.

growth begins to be altered first so as to stain orange. It also becomes granular. By the time the penetrating tube begins to enlarge into the typical vesicle, these changes are conspicuous. The penetrating tube may finally break through the sheath entirely and develop without it. But usually some of the cellulose remains as the granular masses of the sheath. As will be seen, under certain conditions the haustoria of Uncinula Salicis have no such sheaths around their haustoria and the sheaths of Erysiphe graminis on Poa do not show any contents, at least in the older stages, nor are the sheaths themselves always present. The extremely minute size of the penetrating tube has been mentioned. The amount of fermentative action of which the haustorium is capable at first is, therefore, only sufficient to provide for the onward growth of the tube. The circle of its effect has not at first a long radius. The distal end of the cellulose thickening is the first to show signs of dissolution. It becomes granular there first. As the haustorium attains larger growth, the digestive powers of the fungus becomes more effective, and that part of the collar coming within the sphere of influence of the ferment is gradually attacked and partly dissolved. It is interesting to find that the membrane by which the sheath, in the majority of cases, is bounded is contributed from the plasmic membrane of the host cell. It has been mentioned

that the thickening of the host wall under the point of penetration does not appear (to judge by its microscopic structure and reaction to stains) to be a swelling of the cellulose in its early stages so much as the quantitative addition of cellulose at that place. The plasmic membrane of the host cell is discernible bounding this thickening from within the cell as more material is added. It is not ruptured by the ingrowth of cellulose - rather it causes the ingrowth by its activity. The area of the plasmic membrane enlarges with the thickening of the wall. It is still recognizable when the haustorium begins to enlarge at its distal end. It still maintains its properties at the stage represented by Fig. 9. In most cases it remains bounding the minute masses of disintegrated cellulose which form the contents of the sheath. Fig. 9 represents the membrane stretched and firm from the osmotic forces at work in the nutrition of the fungus. At a later time it usually suffers injury, and, sometimes, dissolution.

This fungus is not capable of producing the extraordinary dissolution of cellulose which Ward found in the case of Botrytis. Its supply of enzymic material is limited. The sheaths are therefore usually present, though on rare occasions they are not, as in Figs. 7 and 12. It will be shown subsequently that certain haustoria of Uncinula Salicis do not possess sheaths and that this species has a

greater digestive capacity. Nordhausen found (p.23) in infecting leaves with Botrytis spores, that heavy dews so weakened the enzyme of the fungus that penetration was impossible. It may be that when the cell sap of Geranium begins to be absorbed by the young haustoria of Erysiphe, the enzymic material is weakened or largely reabsorbed. Thus it can be seen how the sheaths with their bounding membranes are possible and how, as De Bary observed long ago, the host cells escape with so little injury.

It is often not possible to determine the hyphae from which the haustoria arise. In the process of imbedding and fixing, the hyphae are easily broken away from the haustoria. So, too, it is difficult to find cases where the nucleus is in a position to pass down the penetrating tube into the haustorium. I have figured the few cases observed, but it cannot be said that these are the nuclei which are ultimately to find their way into the haustoria. The nuclei of the hyphae are sometimes greatly elongated and narrowed. It must be in such a form that they make their way through the penetrating tube.[1] (Fig. 14).

Since it is difficult to represent in a drawing the crowded condition of some of the cells, because of the number of haustoria in them, the photograph of a hair containing several haustoria is added(Fig. 38).

I have, further, investigated Erysiphe graminis on

1. See also figures by Harper. Ref. on p. 663.

Poa pratensis. It has long been known that the haustoria of this species are "branched in a peculiar manner." This fungus grows very luxuriantly on the grasses and fills the epidermal cells full of large branched haustoria. A shiny, colorless area occurs about the penetrating tube (Fig.20), which is slightly larger than that in E. communis. This colorless area is slightly depressed as already mentioned. The collars of cullulose are relatively thick also. Fig. 21 represents about the maximum thickness of the collar for Poa. The body portion of the haustorium is always approximately cylindrical or ellipsoidal with finger-like projections growing out from the ends or sometimes from only one end (Figs. 21 to 23). A large nucleus lies near the middle, and, in either end, in mature examples, there is a large vacuole. The branches are also vacuolated. The body is not always symmetrical with respect to the neck (as in Fig. 22), but the neck may be near one end from which also branches may arise. No cases have been observed where the sheaths contain any granular contents. The sheaths are usually present, but they exhibit great irregularities. Sometimes they are not to be seen except for a short distance around the haustoria; sometimes they completely surround the haustoria, being discernible even down between the branches. At other times the branches penetrate the sheath. The protoplasmic contents of the epidermal cells

are usually scanty. It seems impossible that the cell nucleus should escape destruction when the infesting organs are thus provided with long branches, but the same indifference to the nucleus appears here as in other cases. Even when a cell contains several haustoria (as illustrated by the photograph- Fig. 38), the nucleus is unmolested usually, and often normal in appearance as in cells uninfested. This form of absorbing organ may be looked upon as the result of a special effort of this species to put itself in the way of as much food as possible. The heavy growth of mycelium and the immense number of conidia produced by this species speak for the success it has attained. The appressorium in Fig. 9 would agree with De Bary's h. appenddiculata. Long infested blades frequently show signs of disease. "In California it has been destructive to wheat."[1] Certainly these organs give the impression of rapacity not gained in other Erysipheae.

Other species of Erysiphe. The habit or structure of the other species of E. mentioned on page 53 do not vary so much from the account given of E. communis that a detailed description is necessary. Basal (and even higher) cells of hairs are especially favorable places for the study of haustoria. Figs. 17 and 19 represent such cells from the

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1. Ellis and Everhart. Ref. on page 15. I have never found it difficult to collect material with ascospores developed, in August and September.

hairs of Eupatorium perfoliatum (E. Cichoracearum). In Fig. 16 the host nucleus seems to be disorganized and to lie between the two larger haustoria. The cell is slightly plasmolyzed. In Fig. 18 the host nucleus lies at the base of the collar in a condition not different from that in other hairs. The dark globules (stained red in the sections) do not seem to be degeneration products due to the action of the fungus, but are rather due to the action of the fixing reagents. This plant, it is well known, contains a volatile oil and a resin and it is probable that the globules are connected in some way with these substances. It is very common to find such products in leaves at the time of the year when these materials were gathered.

Uncinula Salicis on Salix discolor exhibits peculiarities in its appressoria and haustoria, which have not, apparently, been heretofore reported. De Bary (Beitr. etc., p. 27) examined U. adunca (now U. Salicis). He gave the name haustoria lobulata to its appressoria, but he did not report any peculiarity in the haustoria. Galloway's paper (cit. p.) concerns U. spiralis (U. Necator). It has frequently been stated, first of all by De Bary and later by others, that the Erysipheae always confine their absorb-[1]

1. De Bary (cit.p.). Tubeuf. Pflanzenkrankheiten. 1895. p. 188. Winter in Rabenhorst's Kriptogamen Flora II Abth. 1887, p. 22. Lindau in Die natürl. Pflanzenfamilien I,1 p.326. Kerner. The Natural History of Plants. Trans. by T.W.Oliver,I,p.166. II. 59,677. 1895. Frank (cit. p.)p.555. Ellis and Everhart. (cit. p.) p. 2. Léveillé, Ann.sc.nat. Ser.III, T.XV.

ing organs to the epidermal cells of the host. Palla (l.c.p.68) has recently shown that this conception is incorrect for the genius Phyllactinia. Uncinula Salicis also offers a striking contradiction to this idea. This species is amphigenous on the leaves of the willow. The means by which this fungus reaches the interior tissues of the leaves is different from that employed by Phyllactinia. On the upper surface of the leaf, Uncinula Salicis sends out, from its lobed appressoria, penetrating tubes into the epidermal cells. But not all of these tubes develop in the epidermal cells into haustoria. Some of the tubes (a little less than half) continue their growth entirely through the epidermal cells of the host into the palisade cells. When these cells have been reached, the distal ends of the penetrating tubes enlarge to form haustoria which do not appear to differ greatly from the ones in Erysiphe communis. On the under surface of the willow leaf the epidermal cells are likewise penetrated by the slender tubes, some of which enlarge in the epidermal cells into haustoria, while about an equal number penetrate into the mesophyll cells immediately under the epidermal cells (Figs. 24 and 26). The figures here all represent cells on the under side of the leaf. As only a part of the haustoria terminate in the epidermal cells, the slender tubes, extending across, give to the epidermal cells which are penetrated by several such tubes

the peculiar appearance of possessing trabeculae. The appressorium of U. Salicis is also peculiar. It does not give rise, as the appresorium of Erysiphe does, to a single haustorium, but usually, two or more haustoria spring from the same appressorium. (Fig. 24 to 30). The haustoria, therefore, sometimes pass through the epidermal wall close together,- a circumstance which adds to the difficulties of studying them. The appressoria of U. Salicis are further peculiar, in that they are not always appressed closely to the epidermal cells. (Figs. 25 to 29). It is to be seen that their penetrating tubes have a longer or shorter growth before they penetrate into the leaf. All of these peculiarities give to the absorbing organs of this species a very striking appearance. It grows with great luxuriance on the willow, as is well known, and its haustoria are very numerous. As far as has been observed, the haustoria are not occasionally septate as in Erysiphe communis. In the possession of a single nucleus surrounded by spongy protoplasm, and in its general shape, a haustorium of Uncinula is not different from one in other genera. The possession of the long necks which reach the subepidermal cells of the host give these haustoria a peculiar structure. The necks are usually straight and slightly larger than the penetrating tubes already described. Occasionally it can be demonstrated that they are accompanied

by the collar of the host cellulose. Within the palisade cells the sheath is discernible about the body of the haustorium, but in the epidermal cells of the leaf the sheaths are inconspicuous or absent. Since Uncinula Salicis makes more use of enzymic materials, in its habit of penetrating further into the leaf than other genera do, it can be understood why the sheaths are less common in this species than in E. communis. It more completely destroys the sheaths.

It might be supposed that, where an intercellular space occurs between two subepidermal cells, the penetrating tube might travel farther into the interior of the leaf. Haustoria have not yet been found, however, deeper than the subepidermal cells.

Palla (l.c.p.68) has very recently reported that Phyllactina[1] has the interesting habit of sending nutrient hyphae through the stomata into the intercellular spaces of the infested leaves. Haustoria are thus constructed en-

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1 It seems worthy of mention that on mature perithecia, the appendages in this genus do not extend parallel to the surface of the leaf, as in the young stages, but obliguely downward. The result is that the perithecia are raised up into the air for the length of the appendages. This causes the perithecia to fall off easily in handling the leaves, and it may be that this is due to an effort at distribution on the part of the fungus.

tirely on the interior of the leaf[1] and are not found in the epidermal cells of the leaf as in Erysiphe. In description of the hemiendophytic habit of this genus Palla writes: "Die auf der Epidermis vegetirenden Phyllactinia-Hyphen durchboren nicht die Epidermiszelle, sondern treiben durch die Spaltöffnungen Seiten-hyphen in das Intercellularsystem des Schwammparenchyma; erst die intercellulären Hyphen bilden in den Schwammparenchymzellen Haustorien aus." Because of the difference in the mode of life he suggests (p. 71) the separation of this family into two groups, the Erysipheae and Phyllactineae. Upon the ground of certain differences, in the appendages of the perithecia, chiefly, he gives the name (p. 65) P. Berberidis to the fungus on Berberis, as contrasted with P. suffulta on leaves of Corylus Avellana. No effort has been made to compare the material collected for this investigation with Palla's results for systematic purposes, but I can confirm most of his observations on the intercellular hyphae and haustoria. Palla

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1. That this fact had not been learned long before is to be accounted for by the fact that investigators interested in the structure of the Erysipheae chose for study a more common genus; Writers who conceived of the Erysipheae as purely epiphytic or as receiving their nutriment entirely from the epidermal cells have been cited (p.). See also Saccardo. Sylloge Fungorum I. 1. 1882. Schauer. Handbuch der Pflanzenkrankheiten. II Th: p. 314, 1886. Tavel, Vergleichende Morph. der Pilze: 74, 1892.

finds that the haustoria on the intercellular hyphae pierce the mesophyll cells in the case of the two hosts he examined. As shown from a study of several hosts, Corylus, Fraxinus, Crataegus, Cornus, used in this investigation, haustoria are produced in the loose porenchyma in a minority of cases. Usually the hyphae penetrate first to a region intimately associated with the fibro-vascular bundles (Figs. 31, 33), before producing absorbing organs. Sometimes haustoria are constructed in the cells binding the bundles to the palisade cells and sometimes in the palisade cells themselves. In Xanthoxylum, however, haustoria frequently penetrate the loose parenchyma cells, (Fig. 34.) Fig. 36 shows the two ways in which the intercellular hyphae may enter the stomata. Except when the nutrient hyphae arise as a side branch immediately over the stoma, it is impossible to determine whether we have to do with an original germinating tube or not. If the stomata stand wide open the initial cell of the penetrating hypha is not narrowed (figs. 33,24), but upon the closing of the stomata the initial cells accommodate themselves to the space left to them by narrowing at the middle and becoming large at the inner end (Figs. 33, 36, 37). Palla finds that the intercellular hyphae of P. suffulta contain at most three cells (p. 70) and of P. Berberidis, two - seldom three or more. Those hyphae in the leaves examined

in this investigation varied with the distance traveled before the production of an absorbing organ. Less than two cells were not found. The number is typically more - three to five. The distal cell is sometimes extremely long, and it is possible that, in tracing its sinuosities through several sections, septa and nuclei may be overlooked which would raise the number of cells above five. When the hyphae produce their absorbing organs near the stomata these hyphae are noticeably larger than the surface hyphae, but when they extend a long distance through the intercellular spaces of the leaf, some or all of the cells are more or less attenuated (particularly the distal cell). An intercellular hypha may sometimes be so long as to extend through twelve or more sections. Haustoria do not appear to be developed exclusively from the side as Palla observed (p. 70), but frequently from the end, as in Figs. 31 and 35. Palla observed hyphae passing into the palisade layer but he did not find haustoria there. In all the hosts mentioned, except Xanthoxylum, the haustoria agree in structure with those of E. communis. Fig. 31 was included because it shows the intimate connection of haustorium and bundle. It also arises from the end of a hypha and contains a crystal so large as to distort it.

The haustoria of Phyllactinia on Xanthoxylum Americanum offer some striking differences in comparison with

those just described. The intercellular hyphae have thicker walls; the intercellular appressoria are conspicuous, flattened, sucker-like structures tightly appressed to the cells of the leaf; the haustoria are very different from any yet described (Figs. 34, 35). Associated with these differences are evidences of a peculiarity in the method of nutrition of the fungus not hitherto described for the Erysipheae. The leaves of Xanthoxylum have a thin layer of loose parenchyma. The bundles are near the lower epidermis. No part of the leaf, therefore, is far from the bundles. These facts of structure seem to influence the parasite. Its intercellular hyphae, as a rule, are short and the cells are thick. They are more vigorous in their appearance and less delicate, and they stain more easily than the surface hyphae. Since the host leaves are thin the intercellular hyphae are shorter than in those hosts where the haustoria are developed far from the stomata. Appressoria are numerous and conspicuous. Even beyond the point where the haustorium is produced the hypha may adhere as an appressorium to the host cell. (Fig. 34). The chief point of interest in this fungus, however, is the noticeable absence of typical haustoria. Long search through many sections has brought to view only one doubtful case of an absorbing organhaving the structure typical for haustoria of the Erysipheae.There are numerous absorbing organs, on the other hand which have the structure

represented in Fig. 34 and 35. The penetrating tubes which pierce the host cell walls are as minute as in the haustoria of Erysiphe, but the vesicles within the cells appear to contain no protoplasm or nuclei. The most conspicuous feature is their thick, shining walls which, in exactly longitudinal sections, appear to be continuous with the walls of the host cells. It was supposed at first that they were young haustoria different in details of development from those of Erysiphe; but their abundance and the many weeks for which the prickly-ash bush must have been infested when the material was gathered make it evident that these are modified haustoria. It is to be seen that there is some resemblance between Figs. 34 and 35 and the early stages of penetration represented in Figs. 2 and 3 from Erysiphe.

Many of the parenchyma cells of the Xanthoxylum leaves are studded over on their exteriors with little globules which look dark under the microscope and are often stained violet. These structures may have been described before though I have not found reference to them. Another striking appearance is the presence of large spherical masses of needle-crystals in the intercellular spaces of the mesophyll cells, with smaller masses in the interior of the cells everywhere, especially in the lower epidermis. These crystals are in addition to the large crystals of cal-

ciumoxalate, well known to be present in these leaves.[1] To ascertain whether these needle-crystals were calcium carbonate, a coverglass was placed on microtome sections which had been fixed to the slide but not yet stained. The crystals were treated then with strong acids and the reaction watched under the microscope. The crystals were not affected by the acids (sulphuric and hydrochloric). The prickly-ash has received much attention from pharmacologists. It produces gum, a crystal resin, a bitter extractive, sugar, and tannin.[2] Without doubt the needle-crystals mentioned have to do with some of these organic substances.

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1. Engler, A. Rutaceae in Pflanzenfamilien. III,4,-.98.

2. In the Amer. Journal of Pharm. see: Lloyd, May, 1890. Eberhart, Ibid. Staples, Oct., 1892. Griffith, 1837. Maisch, p. 226, 1876, Colton, p. 161, 1880. Moffit, p. 417, 1886.

For literature on the structure of Xanthoxylum: Engler. Studien über die Verwandschaftsverhältnisse der Rutaceae, etc. Abhandl. d. naturf. Ges. z. Halle XIII, 2, 1874. Rauter J. Zur entwickelungsgeschicte einiger Trichomgebilde. Wein, 1874. Martinet. Organes de secretion des vegetaux. Ann. sc. nat. 5 Ser. XIV: 94-232, Pl. VIII-XXI.

The crystals are at times so large as to include two or three of the parenchyma cells. Sometimes the intercellular hyphae of the fungus pass through these crystals. In such cases the hyphae show little or no stainable protoplasm, but they are not collapsed.

GENERAL CONSIDERATIONS.

The phenomena exhibited by the intercellular hyphae of Phyllactinia are interesting in connection with what has been ascertained by several investigators in relation to the nutrition of fungi. It has been mentioned that the majority of the intercellular hyphae of Phyllactinia in several of the hosts investigated (except in Xanthoxylium) take a more or less direct course to the regions near the bundles. It was long ago established by Bachs, that the parenchyma sheath around the bundle forms the line of transportation for the soluble carbohydrates. The development by the fungus of the absorbing organs in regions abundantly supplied with available food material indicates a selective chematropism[1] in the fungus. A selective reaction was demonstrated by Miyoshi[2] for Phyllac-

1. The fact of chematropism among fungi is too well established to require discussion here. Büsgen was among the first to investigate this question. Cit. on p. Also
2. Der Honigthau. Jenaische Zeitschr. für Naturw. 1891. Reinhart, Jahrb. für wiss. Bot. XXIII: 4, 1888. Woronin, Mem. de lacad. de St. Petrbg. sec. 7, pl. 36.

tinia offers, under normal conditions of growth, a demonstration of this selective chemotropism which Miyoshi demonstrated by artificial means. This reaction enables Phyllatinia not only to surround itself with conditions which will insure it an uninterrrupted supply of food not insured to it while living as a purely epiphytic parasite, but to find within the leaf of the hosts those regions better supplied with food than the loose parenchyma. If the hyphae are stimulated to place haustoria in cells binding the bundles to the palisade layer, or if haustoria enter the latter, they are still at the very source of that supply of food by which the plant maintains its vigor and activity. The proportion of cases to be found in which the intercellular hyphae do develop haustoria in these more favorable regions is larger than casual observation would lead one to think. By a study of the structures of the host leaf in sections following and preceding the sections containing the examples, it may often be determined that the fungus actually has placed its absorbing organs either in the parenchyma cells constituting the sheath or in cells uniting the bundles to the palisade cells. It should not be thought, however, that the fungus follows this practice invariably. In Xanthoxylum the leaves are so constructed that the bundles are near the lower epidermis which contains the stomata through which the fungus finds access. All of the meso -

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phyll cells therefore have a surplus of food. This fact would account for the number of mesophyll cells which contain haustoria.

It is important to discover how far parasitic fungi make use of saprophytic methods. I have mentioned that Phyllactinia on Xanthoxylum showed some evidence of a peculiarity of nutrition not hitherto ascribed to the Erysipheae. This species gives the impression that it is nourished in part by the material in the intercellular spaces of the leaf. The peculiar, ovoid form of its haustoria and the abundance of material present in the intercellular spaces first suggest the idea. These points are not of themselves proof, for the ovoidal haustoria of this species may be especially adapted for absorption. It is noticeable, however, that when, within the tissue, the intercellular spaces or other parts of the host block the way, the hyphae of the fungus are thin, clear and vigorous, but that the haustoria are pressed into, and also when the hyphae take haustoria at some distance from the stoma. The hyphae which do not enter the cells, but run between them, frequently touch the cell walls, but the haustoria are rarely found on these hyphae. They are less vigorous in appearance. If this is the case, as the hyphae in such a case lack the characteristic haustoria, Fig. 37, perhaps this may be the reason why the hyphae do not

strated by

phyll cells therefore have a surplus of food. This fact would account for the number of mesophyll cells which contain haustoria.

It is important to discover how far parasitic fungi make use of saprophytic methods. I have mentioned that Phyllactinia on Xanthoxylum showed some evidence of a peculiarity of nutrition not hitherto ascribed to the Erysipheae. This species gives the impression that it is nourished in part by the material in the intercellular spaces of the leaf. The peculiar, modified form of its haustoria and the abundance of material present in the intercellular spaces first suggest the idea. These points are not of themselves proof, for the modified haustoria of this species may be especially adapted for absorption. It is noticeable, however, that when, within the stomata, the intercellular hyphae encounter parenchyma cells which block the way, the cells of the hyphae are short, thick and vigorous; not only when haustoria are produced near, but also when the hyphae have haustoria at some distance from the stomata. But the hyphae which do not encounter such cells, but run a comparatively uninterrupted course before constructing haustoria, are more or less attenuated and are less vigorous in appearance. If some cell of the hypha in such a case lies in contact with a parenchyma cell(Fig. 37, penultimate cell), that cell of the hypha is short,

thick and vigorous. Büsgen (l.c), in germinating conidia of Erysiphe, found that the germinating tubes had a limited growth under the conditions he was able to establish. He did not succeed in infecting pieces of leaves arranged for the purpose. If, under natural conditions of infection, the germinating tubes have a limited growth unless supplied with nutrient material from the host in some way, it is not clear how they can grow down into the leaves for comparatively long distances, as they sometimes do, before producing haustoria, unless they do appropriate intercellular material.

This last point is important but it cannot be applied without reservation until infection phenomena have been observed more in detail than has yet been possible. It is possible, of course, that the first side branch into the interior of the leaf makes haustoria near the stoma and thus supports the whole branching hypha until other side branches in other stomata are able to assist.

There is evidence to support the possibility of intercellular nutrition in this fungus. Miyoshi's observations[1] illustrate the extreme sensitiveness of fungi to chemotropic stimuli. Nordhausen[2] has shown that

1. Ueber Chemotropismus der Pilze. Bot. Zeit. 1894. pp. 1-28 Tf. I. Ueber Reizbewegungen der Pallenschläuche. Flora oder allg. Bot. Zeit. Heft I. 1894. Die Durchbohrung von Membranen durch Pilzfaden. Jahrb. f. wiss. Bot. B. XXVIII. H. 2: 1895, p. 269.
2. Beiträge zur Biologie parasitärer Pilze Jahrb. f. wiss. Bot. B. XXXIII. 1898. pp. 1-46.

Botrytis, which is usually saprophytic, can under favorable conditions be made to infect Tradescantia, Nnium etc. Marshall Ward (l.c. pp. 348-354) believes that the Botrytis which produced the lily-disease he describes, may live as a saprophyte as well. He was able to grow the fungus for a series of weeks in nutrient solutions. Brefeld[1] has shown that saprophytes like Penicillium and Mucor play an important part in the rotting of fruit. Büsgen (l.c. p. 67) believes that the yeasts which infest fruit first live for a time on the exterior on the small amount of nutrient material exuding on the surface. To prevent this attack appears to be the function of the waxy exterior so common in fruits. He removed the bloom from grapes by means of running water and found later upon immersing them in water in which bacteria were growing that these multiplied very rapidly upon the food coming from the interior of the grapes through the skin. By another experiment he found that bacteria found abundant material exuding from the surface of leaves at the cross-walls. Büsgen (l.c.p.66) observed that the hyphae of Uromyces on Sedum are larger and more vogorous around and in the stomata through which they penetrate. By several control experiments he shows that an abundant supply of food is present which the fungus may use. He concluded that Uromyces is partly saprophytic,

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1. Sitzungsber. d. natürf. Freunde. 1875.

and that the enlargement of the hyphae in the stomata is the result of chemical stimuli. Frank[1] observed similar phenomena in Cercospora. All of these results assist in bridging over the gulf which has been supposed to exist between saprophytes and parasites. Nordhausen (l.c.p. 23) observed in infecting leaves with Botrytis that after heavy dews the intercellular spaces of the leaves were flooded with water. He thinks the solution of intercellular material in this water offers chemotropic stimuli to parasitic fungi. My observations do not warrant me in concluding that other forms of Phyllactinia, aside from the form on Xanthoxylum, use intercellular nutrition. Nor is it probable that the fungus on Xanthoxylum depends upon such a food supply chiefly. It produces absorbing organs which, as far as I can discover, are different from the typical form. But it cannot be concluded that these are not functional, whether they are modified by lack of use or whether by the reaction of the host. Nor does the production of ordinary haustoria exclude this mode of nutrition in those hosts which offer suitable conditions for it.

It should not be assumed that the nutrient hyphae are greatly specialized. As I have shown, the cell between the guard cells assumes such forms as are permitted by the stomata at different times. I have also shown that the

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1. Pflanzenkrankheiten, p. 596, and Bot. Zeit. p. 40, 1878.

number of cells in the hyphae is variable.

There are two points connected with my observation of the Erysiphe on the Geranium-leaf which may be mentioned briefly. On one occasion, (at the end of a section where the scissors with which the pieces of leaves were cut had destroyed the section in part) I found a haustorium in what was clearly a subepidermal cell. Its connection with the surface was destroyed, but there is no doubt that it was a normal haustorium in one of these cells. Whether it was due to the chance presence of Phyllactinia on this host, whether Erysiphe occasionally adopts the practice of Uncinula Salicis, or whether it was Uncinula itself on this host, I have not determined. With this circumstance is related a note on page 9 of Ellis and Everhart's N.A. Pyrenomycetes. This note corrected the mistake of the artist (T.W. Anderson) who, it is supposed, wrongly represented a germinating tube from a conidium of Sphaerotheca Castagnei as entering a stoma (pl. I, Fig. 3). It is due to the artist to state that he probably saw this, but whether it was a tube of Phyllactinia or whether this species has a similar habit to Uncinula, I have not determined.

A very curious condition is observable in the most of the cells of the Geranium-leaf, external and internal. They appear at first to possess no vacuoles. The whole cell appears to be filled with a delicate, spongy proto-

plasm staining orange or sometimes very slightly violet. The contrast in structure between this and the ordinary protoplasm is marked. As may be seen from a comparison of the different host cells accompanying this paper, whatever cellsap was present in the vacuoles of the cells of the other leaves was removed in the process of fixing and staining. But here the cell sap possesses some constituent which is precipitated or coagulated by the fixing solutions and which remains as a permanent product in the sections. Closer inspection shows that it differs from the ordinary protoplasm which can be seen in various positions in the cells. Thus, in figures 7, 9, and others, the cell protoplasm is confined to the neighborhood of the plasmic membrane, with larger or smaller aggregations in the corners of the cells, and often in connection with the haustorium. Bars and bands of protoplasm are seen extending from the sheaths of the haustoria to various parts of the cells, between which this minutely spongy, slightly violet mass is present.

It is a pleasure to acknowledge the assistance I have had in this investigation from Professor C. R. Barnes, under whom the work was begun, and from Professor R. A. Harper, under whom it was largely accomplished.

LIST OF GENERA AND SPECIES STUDIED.

ERYSIPHE.

E. communis, (Wallr). on Geranium maculatum, L.

E. graminis, D.C. on Poa pratensis, L.

E. Galeopsidis, D.C. on Scutillaria lateriflora, L.

E. Galeopsidis, D.C. on Galeopsis Tetrahit, L.

E. communis on Polygonum Aviculare, L.

E. Cichoracearum D C.on Eupatorium perfoliatum, L.

SPHAEROTHECA.

S. Castagnei, Lev., on Bidens cernua, L.

PODOSPHAERA.

P. Oxycanthae, D C. on Prunus ? .

MICROSPHAERA.

M. Russelii, Clinton, on Oxalis corniculata, L. Var. stricta Sav.

UNCINULA.

U. Salicis, D C. Wint., on Salix discolor, Muhl.

U. necator, Schw., on Vitis? .

U. Clintonii, Peck, on Tilia Americana, L.

PHYLLACTINIA.

P. suffulta, (Reb.),[1] on

Fraxinus pubescens, Lam.;

Crataegus punctata, Jacq.;

Xanthoxylum Americana, Mill. (X. Fraxineum, Willd.);

Corylus Americanum, Walt.

Cornus stolonifera, Michx.

Such forms as are not discussed in the preceding pages have not been found to differ so materially from Erysiphe communis as to require a separate discussion of their haustoria.

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1. I have not examined my material with reference to the classification of Phyllactinia proposed by Palla (l.c.p.65). I therefore group all these under P. suffulta.

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EXPLANATION OF FIGURES.

All the figures were drawn by the aid of the Abbé camera lucida.

Magnification of figures 8, 11, 13, 24 to 30, 900 diameters; figures 16, 18, 19, 32, 2000 diameters; figures 36 2nd 37, 400 diameters; all other figures 1800 diameters.

Figs. 1-15 Erysiphe communis on Geranium maculatum.

Fig. 1. First stage in penetration, marked by spot on inner surface of host wall.

Fig. 2. Penetrating tube just beginning to make its way through epidermal wall. Wall thickens as tube grows.

Fig. 3. Having enlarged at a point in line with the inner boundary of the epidermal wall the tube continues its growth.

Fig. 4. Further stage in penetration. Cellulose papilla elongates as tube grows. Distal end of cellulose ingrowth begins to show signs of disintegration. Nucleus of host cell on basal wall of cell.

Fig. 5. Distal end of penetrating tube now begins to enlarge. Cellulose further disorganized. The proximal end of ingrowth not disintegrating, but is destined to remain as collar about neck of haustorium.

Fig. 6. Young haustorium escapes from cellulose thickening and is developing without sheath.

Fig. 7. Haustorium without sheath.

Fig. 8.. Middle haustorium in optical section. the two at end in longitudinal section. Sheath present about haustoria.

Fig. 9. Stage before entrance of haustorium nucleus. Stretched and intruded plasmic membrane of host cell forms bounding membrane of sheath which in this case is devoid of contents.

Fig. 10. Plasmolyzed cell showing collar as an ingrowth of cellulose from cell wall. Partly in perspective.

Fig. 11. Haustorium with two nuclei. Septum also found across neck.

Fig. 12. Haustorium without sheath. Protoplasm of host cell adherent to sides of neck.

Fig. 13. Haustorium shows septum across neck.

Fig. 14. Elongated nucleus in mycelial hypha.

Fig. 15. Membrane absent about sheath, which here consists of lumps of disintegrated cellulose adhering to body of haustorium.

Figs. 16-19. Erysiphe Cichoracearum on Eupatorium perfoliatum.

Figs. 16-18. Basal cells of hairs containing haustoria.

Fig. 17. Shows unstained area about point of penetration. Remainder of host wall staining darkly.

Fig. 19. Epidermal cell with haustoria. Host cell nucleus is on wall of host cell. Sheaths conspicuous.

Figs. 20-23. Erysiphe graminis on Poa.

Fig. 20. See Fig. 17.

Figs. 21-23. Three branching haustoria.

Figs. 24-30. Uncinula Salicis on Salix discolor.

Fig. 24. Epidermal cell containing one haustorium, while from the same appressorium another penetrating tube passes through the epidermal cell into the subepidermal cell. The sheaths are not visible.

Figs. 25-29. Various forms of appressoria giving rise to two or more haustoria.

Figs. 31-32. Phyllactinia on Fraxinus pubescens.

Fig. 31. Haustorium arising from end of intercellular hypha and penetrating parenchyma cell connected with bundle. Haustorium contains a crystal.

Fig. 32. Part of an intercellular hypha. Guard cells drawn apart and hypha not compressed as in Figs. 33 and 36.

Fig. 33. The host is Cornus. Intercellular hypha consisting of four cells. Haustorium arising from side of distal cell. Host cell below palisade cells.

Figs. 34-37. Phyllactinia on Xanthoxylum.

Fig. 34. Modified haustorium arising from appressoria and penetrating mesophyll cell. Host cell shows exudations on its exterior. A second appressorium also shown.

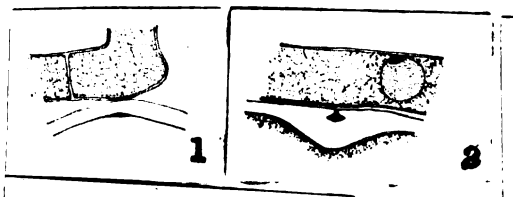
Fig. 35. Smaller haustorium and arising from end of hypha. Exudation on cell of leaf shown.

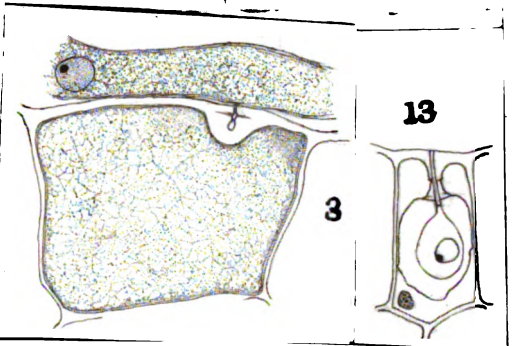
Fig. 36. Stoma containing initial cells of two intercellular hyphae, one a side branch. Origin of the other is indeterminate.

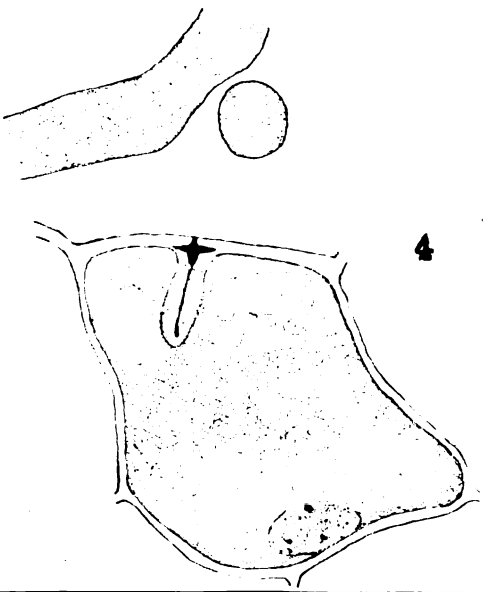
Fig. 37. Shows intercellular hypha with haustorium in cell joining bundle to palisade cell. Middle cell of hypha is short and thick and lies on cells of host.

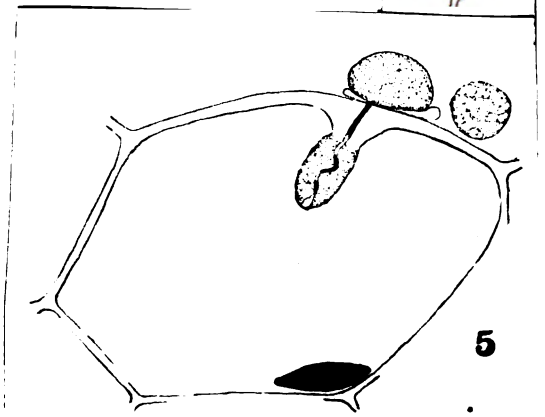
Fig. 38. Photograph of hair showing host cell nucleus and several haustoria.

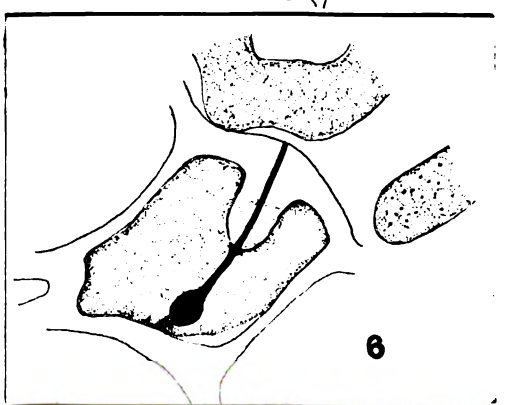
PLATE I

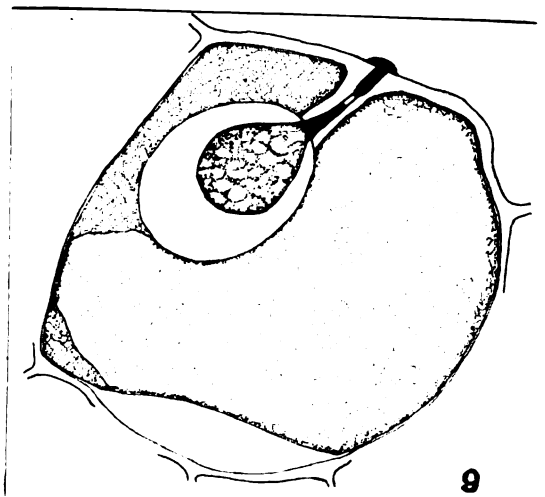


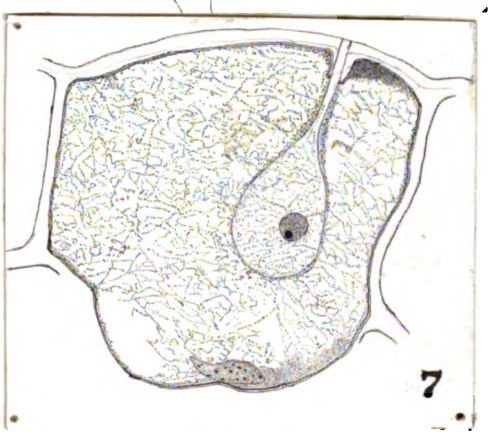












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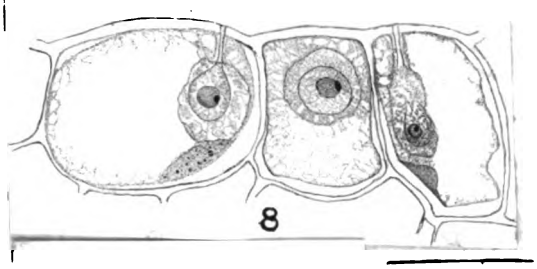

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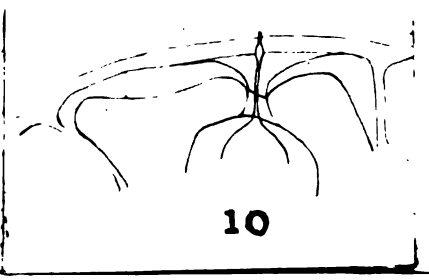

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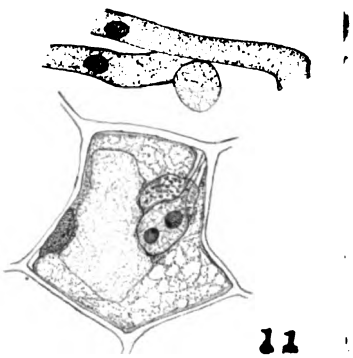

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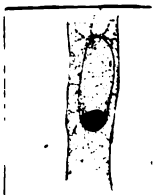

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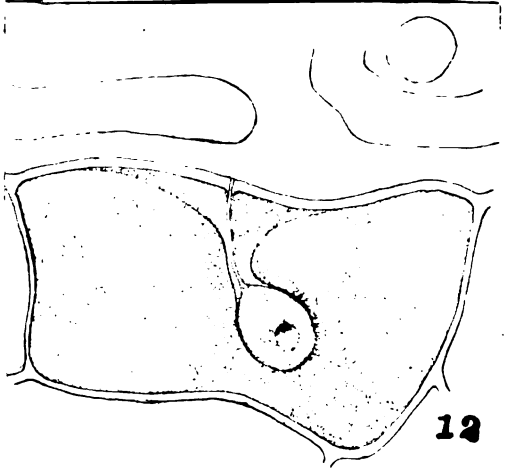

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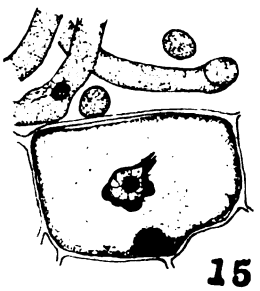

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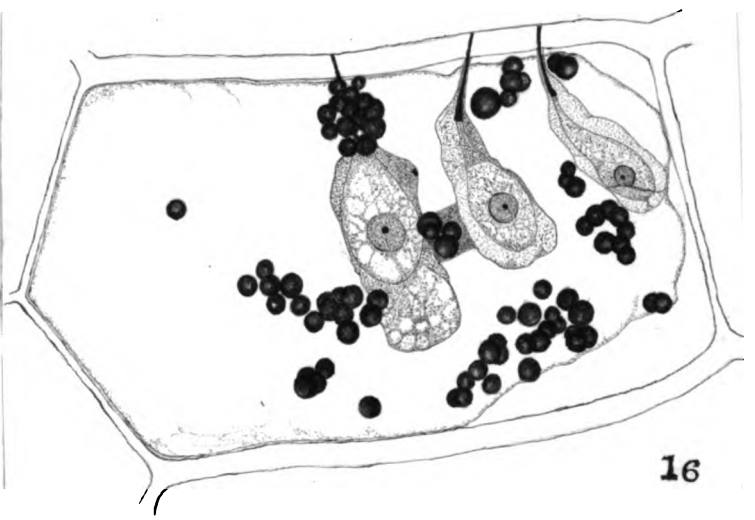

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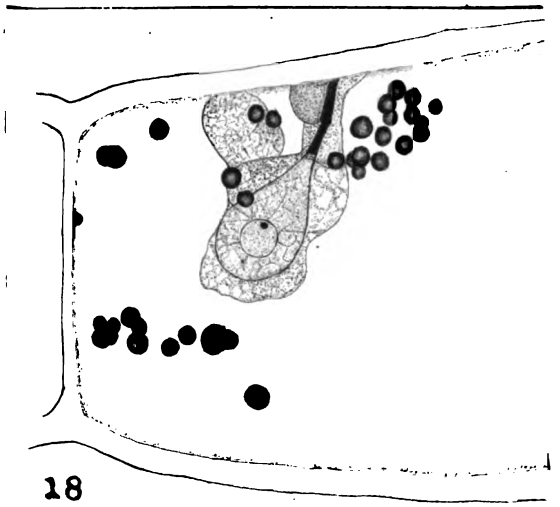
PLATE III.



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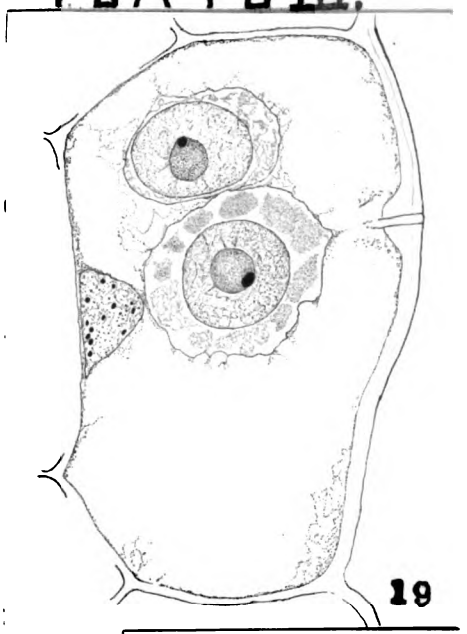

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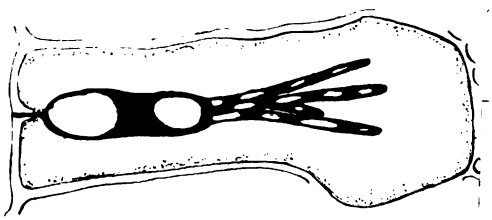

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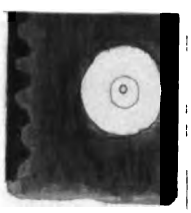

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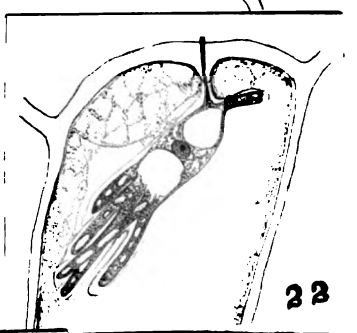

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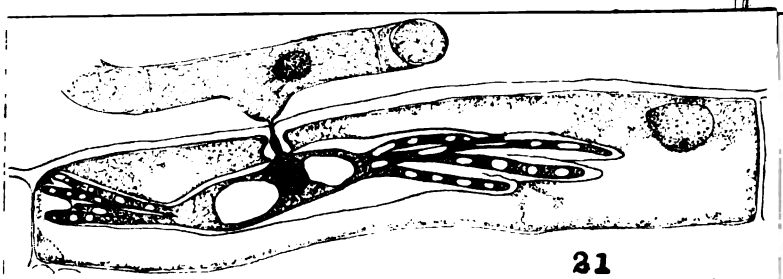

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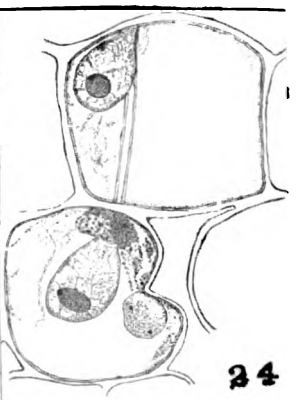

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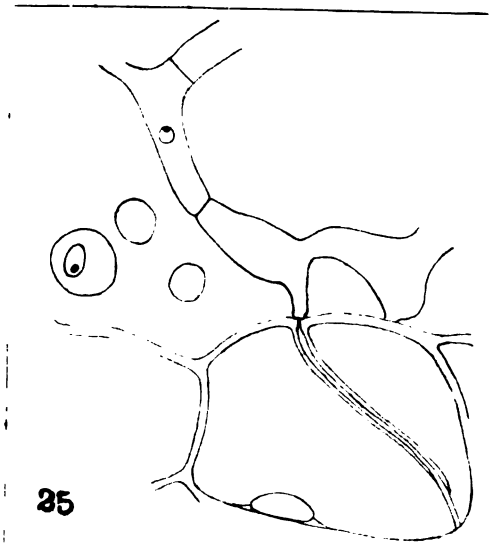
PLATE IV.



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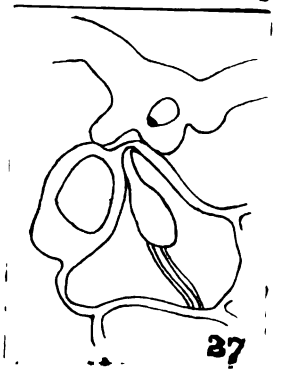

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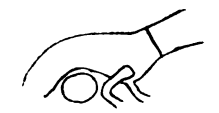

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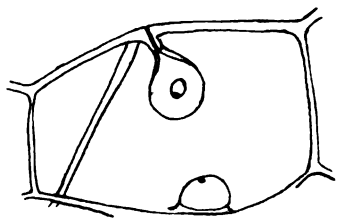

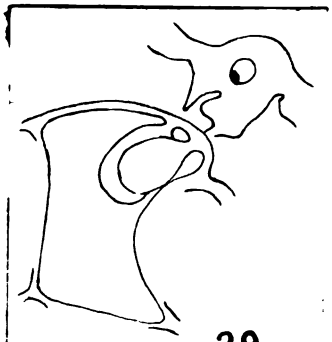

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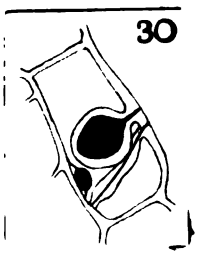

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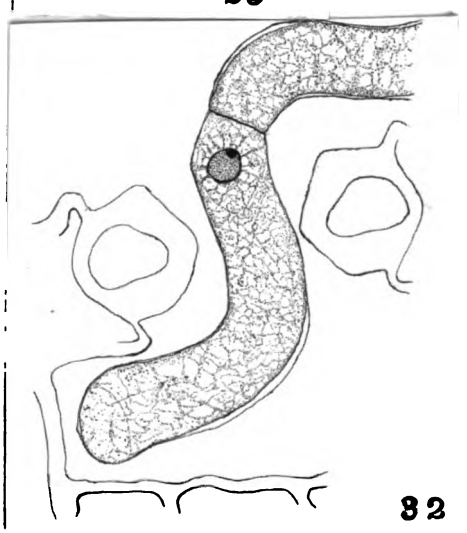

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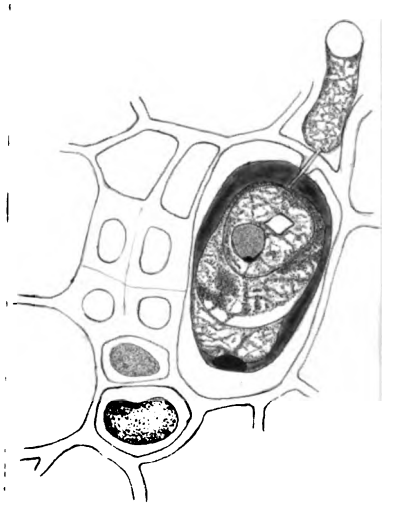

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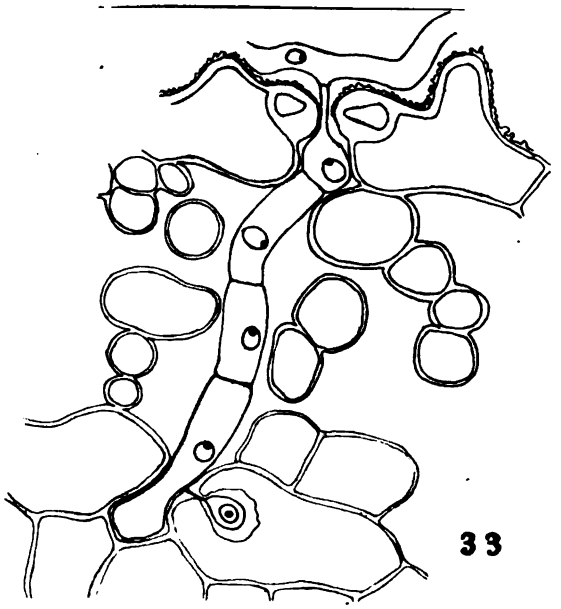

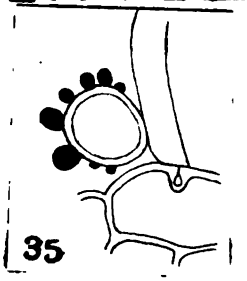

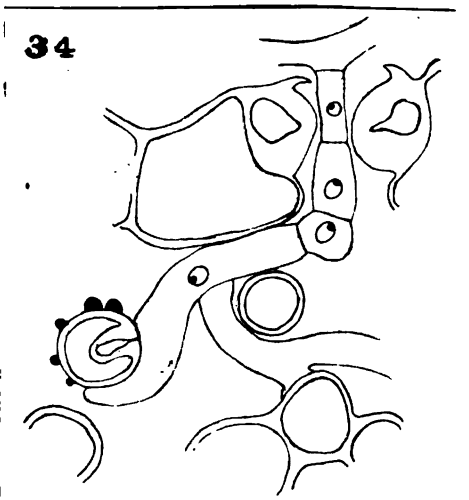

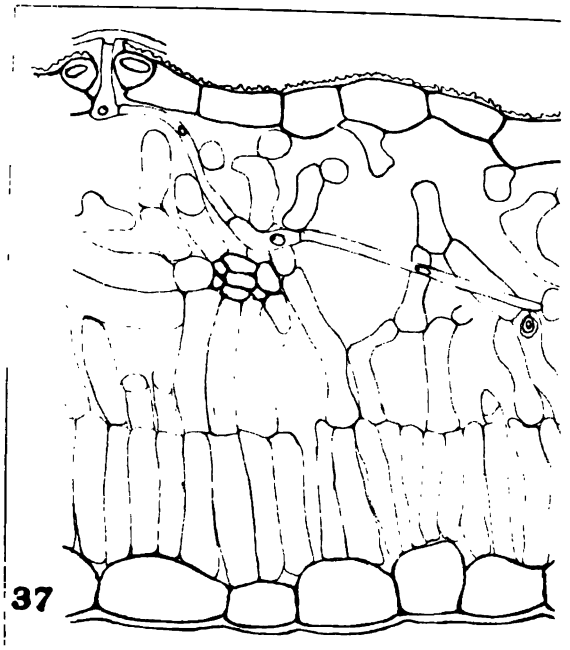

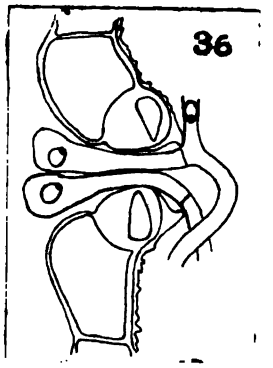

Approved June 13 1899

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